

Preferences of common Central European millipedes for different biotope types (Myriapoda, Diplopoda) in Saxony-Anhalt (Germany)

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Abstract

Knowledge of habitat preferences of myriapod species is essential for their optimal use in bioindication and biological soil assessment. To increase our knowledge a sampling project was started in Saxony-Anhalt (Eastern Germany) more than 20 years ago. The narrowly defined geographic area was selected for the study because the fauna of this Central European German region represents to a high degree the whole of the Central European fauna. The millipede fauna at 175 sites belonging to 12 biotope types was sampled by pitfall trapping and identified to species. According to plant associations, these sites could be divided into four groups differing in moisture and into two groups differing in the level of vegetation cover. Considering the distribution pattern of 28 selected millipede species in each of these groups (weighted percentage), ecological categories of these species could roughly be distinguished. “Main Preferences” separated open land or woodland species and hygrobiont or xerobiont species. The number (and quality) of the occupied biotope types allowed assessment as stenotopic or eurytopic species (“General Preferences”). If available, a “Special Preference” for a preferred biotope type was recognised. For several species, the results are compared with those in the literature.

Keywords

Diplopoda, woodland species, open land species, biotope type, preference, hygrobiont, xerobiont, eurytopic, stenotopic

Introduction

In the last 10 to 15 years the protection of structure and function of soil biocoenoses has become more and more a focus of public and governmental interest, and methods for assessing biological soil quality are in demand. Diplopods as saprophagous animals are an essential component of soil fauna. Their role as bioindicators is indisputable. However, before diplopods can be used as optimal indicators for site characterisation, a better knowledge of their environmental requirements will be needed. Laboratory autecological experiments are unfortunately rare (Haacker 1968a, 1970; Rossolimo and Rybalov 1979). On the other hand, valuable information about preferences can be found in field studies in a range of different habitats (Thiele 1959, Ceuca et al. 1977, Dunger and Steinmetzger 1981, Wegensteiner 1982).

Ecological preferences of animals are mostly deduced from characteristics of the habitat in which these animals are living (e.g. sandy/loamy soils, under grasses or woodlands, in open soils, etc.). More detailed information is available from the description of plant associations and their characteristics. To increase our knowledge of diplopod habitat selection, the millipede fauna of different biotope types defined by plant sociological studies in the German federal state of Saxony-Anhalt (Central Europe) was investigated and compared with literature data. The narrowly defined geographic area was selected for the study because the fauna of this Central European German region represents to a high degree the Central European fauna as a whole.

Methods and sites

Material

Over the past 20 years the Senckenberg Museum of Natural History Görlitz (SMNG) has been studying the soil fauna at a variety of sites spread out over the whole area of Saxony-Anhalt (e.g. Voigtländer 2003a-d, 2008a, b, 2009; Voigtländer and Düker 2001). Specimens have been collected by pitfall trapping, with 70 to 360 traps per site and a collecting period of at least one year. For the present study, 175 sites from Saxony-Anhalt were considered. Only species found at more than 10 sites were included in the analysis of biotope type preference. This reduced the number from the 40 species known from Saxony-Anhalt (Voigtländer 2009) to 28, with a total of approximately 27,000 specimens. All material is deposited in the collections of the SMNG.

Sites

Descriptions of sampling sites are based on defined plant associations (= biotope types; see Table 1). Moisture and temperature were chosen as the most important habitat factors determining distribution of myriapods (Haacker 1968a). Four somewhat rough









level of moisture (very wet, wet to humid, dry and very dry) were deduced from known features of the plant associations (Schubert 1960, Runge 1994). Two categories of structure of vegetation cover were distinguished (Table 1), namely multi-level (tree and shrub layer) and single-level vegetation (grassland). Note that the density of a single-level vegetation cover can vary greatly in the course of the year.





Characterisation of the preference of a species

The ecological classification of species was carried out as follows (Fig. 1):

For “General Preferences” (distribution over 12 biotope types) a species was said to be eurytopic or stenotopic. Occurrence in one to five (similar) biotope types defined

Table 1. Description of sampling sites.

Biotope type		Plant association	Number of studied sites	Site characters
	bogs and swamps	Sphagnetalia magellanici Scheuchzerietalia palustris	14	very wet, single-level vegetation cover
	fresh meadows and pastures	Molinio-Arrhenatheretea, Dauco-Arrhenatheretum (fresh formation), Trisetetum flavescens, Angelico-Cirsietum oleracei	8	wet to humid, single-level vegetation cover
	brook- or riversides	Alnus- or Alnus-Fraxinus- and Salix-associations	5	wet to humid, multi-level vegetation cover
	flood plains and swamp forests	Alnetum, Betuletum, Salicetum, Ledo palustris-Pinetum	19	very wet, multi-level vegetation cover
	deciduous and deciduous mixed forests	Fagetalia, Querco-Carpinetum	25	wet to humid, multi-level vegetation cover
	thermophilic woods	Quercetalia pubescenti-petraeae, Tilio-Carpinetum on sandy-loamy soils	6	dry, multi-level vegetation cover
	coniferous forests	Pinetum	14	dry, multi-level vegetation cover
	dwarf-shrub heaths (DSH)	– subatlantical DSH (Genisto pilosae-Callunetum) on nutrient-poor, sandy soil (podsol) – subalpine DSH (Pulsatillo- Nardetum), on granite gravel (Euphorbio-Callunetum, Harz mountain)	9	very dry, single-level vegetation cover

Biotope type	Plant association	Number of studied sites	Site characters
 xeric shrub societies	Berberidion with the association Ligustro-Prunetum spinosae and pioneer forests tending towards the association Potentillo albae-Quercetum petraeae on loamy-mary soils	6	dry, multi-level vegetation cover
 xeric and mesoxeric meadows	– Corynephorion canescentis with Spergulo morisonii-association – Corynephorum canescentis on dry and warm, nutrient-poor inland dunes with loose Pleistocene sand – Armerion elongatae on sandy, dry soils with a more or less multi-level sod – Teucrio-Seslerietum – Festuco-Brachypodietum – Mesobrometum – Festuco-Stipetum	54	very dry, single-level vegetation cover
 special structures	– semi-natural and anthropogenic vegetation-poor sites (clear cutting, granite debris)	5	dry, single-level vegetation cover
 fields and fallows on different soils		8	dry, single-level vegetation cover

a stenotopic species; occurrence in six or more biotope types, a eurytopic species; and occurrences in fewer than six but very different biotope types, a eurytopic species.

“Main Preferences” were deduced from the species distribution along a moisture and vegetation gradient and from an assessment of a species as woodland vs open land and hygrobiont vs xerobiont.

“Special Preferences” refers to occurrence in special biotope types (e.g. mesoxeric meadow, mixed forest).

Calculation

The Main Preference of millipede species at particular site types was determined from their “presence”, which was calculated using the number of different sites of the same biotope-type (within a greater area) at which a certain species occurs:

$$P = 100 \times \frac{S_i}{X_i}$$

P = presence
 S_i = the number of sites in which a particular species occurs
 X_i = the total number of sites

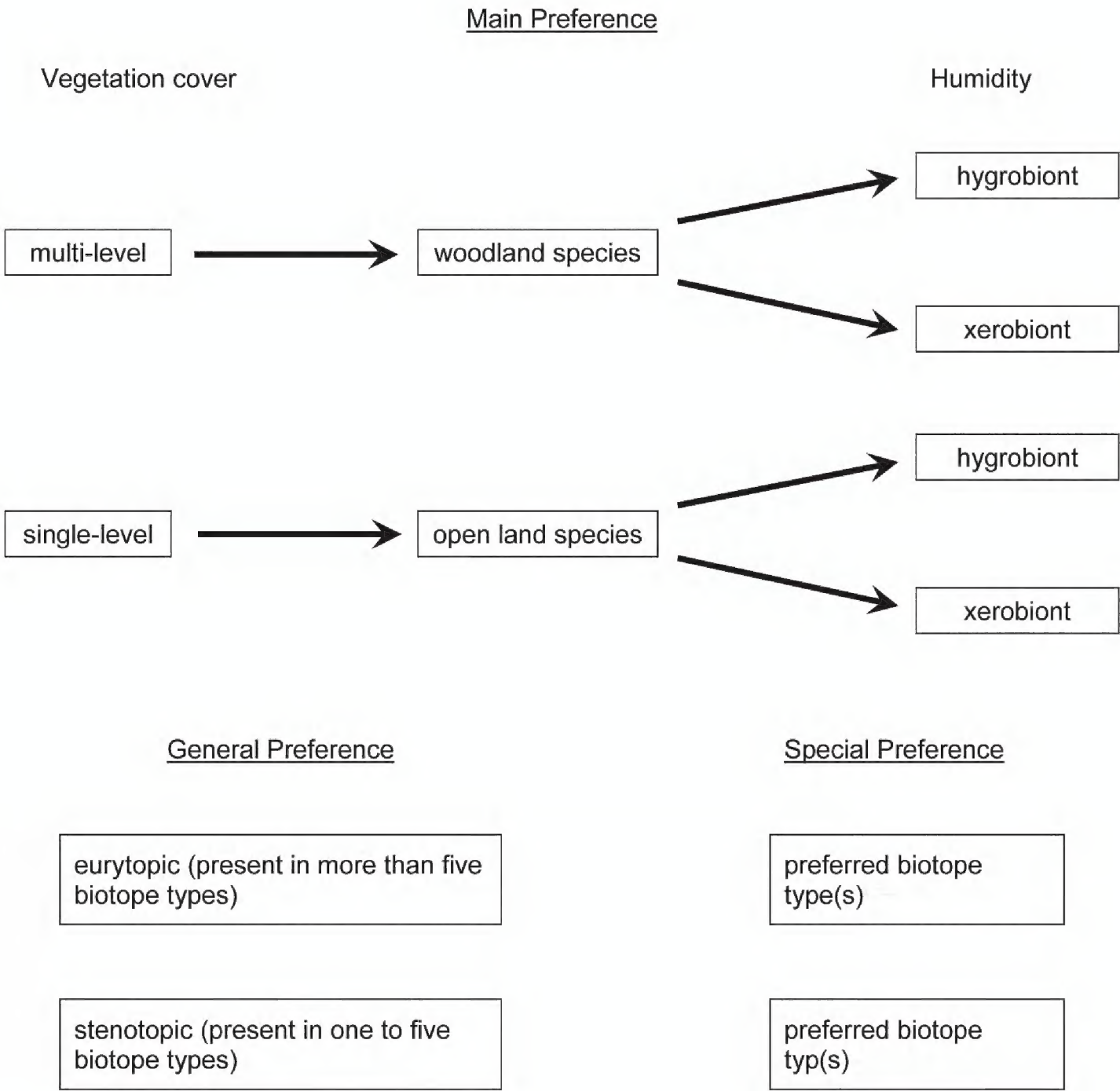


Figure 1. Classification of preferences.

As different site numbers of each biotope type were investigated, a weighting had to be included according to the following formula:

$$P_{\text{rel}} = \frac{\frac{s_i}{\bar{x}_i}}{\sum \frac{s_i}{\bar{x}_i}}$$

Results

General preferences

On the basis of distribution over the 12 biotope types, 20 species can be characterised as eurytopic and eight species as stenotopic (Figs 11, 12, 14, 20, 22, 24, 25 and 27), with stenotopy especially high in open land species. Although *Julus scanicus*, *Megaphyllum pro-*

jectum kochi and *Brachydesmus superus* occur only in five biotope types (Figs 10, 19 and 28) these species are assessed as eurytopic, because the site characteristics differ widely.

Main preferences

Table 2 summarises species distribution along the moisture and vegetation cover gradients of the 175 investigated sites. Eight inhabitant groups are recognised:

Woodland species: Of the 17 species characterised as woodland species, 10 species are hygrobiont (groups II and III) with a preference for very wet biotope types (group II, five species) or wet to humid biotope types (group III, five species). One woodland species, *Leptoiulus belgicus*, is xerobiont (group IV). On the distribution of six species (group I), the moisture level of the biotope types has no apparent influence.

Open land species: Only nine species can be characterised as open land species (groups VI and V), and most of these are xerobiont. Only the occurrence of *M. projectum kochi* is not apparently influenced by the moisture level of the biotope type. Eight species show a clear preference for a combination of very dry or dry biotope types with single-level vegetation cover. Only *Polydesmus inconstans* does not differ between these two moisture categories. One species (*Ophiulus pilosus*) prefers dry, the other six species prefer very dry biotope types (xeric and mesoxeric meadows).

Uncharacterised species: *B. superus* and *Mycogona germanica* do not fit into the scheme of woodland or open land species. *B. superus* is clearly hygrobiont (group VII), while for *M. germanica* no influence of moisture or vegetation cover could be observed (group VIII).

Table 2. Species distribution (groups of Main Preference) along the moisture and vegetation cover gradients of 175 investigated sites using Prel (see above).

	Degree of humidity				Vegetation cover		Family
	very wet	wet to humid	dry	very dry	single-level	multi-level	
Group I Inhabitants of biotope types with multi-level vegetation cover and different moisture (wood-land species)							
<i>G. undulata</i> var. <i>conspersa</i> C. L. Koch, 1847	–	38.67	28.67	32.66	36.84	63.16	Glomeridae
<i>Glomeris marginata</i> (Villers, 1789)	8.02	34.82	19.36	37.80	46.52	53.48	Glomeridae
<i>Glomeris hexasticha</i> Brandt, 1833	19.70	23.96	25.38	30.96	38.71	61.29	Glomeridae
<i>Proteroiulus fuscus</i> (Am Stein, 1857)	30.19	19.66	30.38	19.77	34.43	65.57	Blaniulidae
<i>Leptoiulus proximus</i> (Němec, 1896)	16.75	36.37	33.71	13.16	27.27	72.73	Julidae
<i>Julus scandinavius</i> Latzel, 1884	25.17	31.80	20.26	22.77	33.66	66.34	Julidae
Group II Inhabitants of very wet biotope types with multi-level vegetation cover (hygrobiont woodland species)							
<i>Polyzonium germanicum</i> Brandt, 1831	88.56	4.52	4.19	2.73	11.69	88.31	Polyzoniidae
<i>Craspedosoma rawlinsii</i> (Leach, 1815)	38.05	34.78	17.73	9.44	30.84	69.16	Craspedosomatidae

	Degree of humidity				Vegetation cover		Family
	very wet	wet to humid	dry	very dry	single-level	multi-level	
<i>Polydesmus denticulatus</i> C. L. Koch, 1847	46.44	33.61	14.54	5.41	20.00	80.00	Polydesmidae
<i>Xestoiulus laeticollis</i> (Porat, 1889)	94.53	5.47	–	–	20.00	80.00	Julidae
<i>Julus scanicus</i> Lohmander, 1925	65.69	19.02	–	15.29	31.03	68.97	Julidae
Group III Inhabitants of wet to humid biotope types with multi-level vegetation cover (hygrobiont woodland species)							
<i>Polydesmus angustus</i> (Latzel, 1884)	3.04	50.18	24.48	22.30	30.00	70.00	Polydesmidae
<i>Nemasoma varicorne</i> C. L. Koch, 1844	32.63	47.22	8.75	11.39	15.79	84.21	Nemasomatidae
<i>Allajulus nitidus</i> (Verhoeff, 1891)	11.58	45.27	27.97	15.17	34.18	65.82	Julidae
<i>Tachypodoiulus niger</i> (Leach, 1815)	2.67	55.63	19.33	22.37	31.49	68.51	Julidae
<i>Unciger foetidus</i> (C. L. Koch, 1838)	11.32	55.71	15.19	17.79	29.03	70.97	Julidae
Group IV Inhabitants of very dry biotope types and multi-level vegetation cover (xerobiont woodland species)							
<i>Leptoiulus belgicus</i> (Latzel, 1884)	3.70	28.88	26.77	40.65	45.32	54.68	Julidae
Group V Inhabitants of biotope types with single-level vegetation cover and different moisture (open land species)							
<i>Megaphyllum projectum kochi</i> (Verhoeff, 1907)	41.37	7.19	6.66	44.78	54.50	45.50	Julidae
Group VI Inhabitants of very dry and dry biotope types with single-level vegetation cover (xerobiont open land species)							
<i>Polydesmus inconstans</i> Latzel, 1884	10.33	24.67	31.18	33.82	68.72	31.28	Polydesmidae
<i>Melogona voigtii</i> (Verhoeff, 1899)	14.12	–	34.10	51.78	56.76	43.24	Chordeumatidae
<i>Choneiulus palmatus</i> (Němec, 1895)	6.30	5.47	35.47	52.77	89.61	10.39	Blaniulidae
<i>Ophiulus pilosus</i> (Newport, 1842)	25.13	10.91	60.67	3.29	80.00	20.00	Julidae
<i>Kryphioiulus occultus</i> (C. L. Koch, 1847)	–	–	18.00	82.00	100.00	–	Julidae
<i>Cylindroiulus caeruleocinctus</i> (Wood, 1864)	3.66	28.59	29.44	38.32	60.90	39.10	Julidae
<i>Megaphyllum unilineatum</i> (C. L. Koch, 1838)	0.00	4.00	33.33	62.67	96.33	3.67	Julidae
<i>Ommatoiulus sabulosus</i> (Linnaeus, 1758)	14.93	12.97	24.04	48.05	71.68	28.32	Julidae
Group VII Inhabitants of very wet biotope types and different vegetation cover (hygrobiont)							
<i>Brachydesmus superus</i> Latzel, 1884	48.03	11.92	22.09	17.97	48.39	51.61	Polydesmidae
Group VIII No influence of moisture or vegetation cover							
<i>Mycogona germanica</i> (Verhoeff, 1892)	17.41	30.24	28.03	24.32	51.22	48.78	Chordeumatidae

Special preferences

The distribution of each investigated species over the biotope types can be seen in Figs 2–29. Depending on the level of occurrence, Special Preferences can be recognised.

The biotope type selections of certain species are discussed below.

Combination of preferences

An assessment of the autecology of the species investigated can be derived from a combination of the three preference types (General, Main and Special). An overview is given in Table 3.

Species belonging to group I are woodland species. They are eurytopic, mostly without special preferences for a biotope type. Occurrence in eight to 10 different types is the rule (see Figs 2 to 7). Their occurrence seems to be influenced by the reduction in insolation and temperature (closed tree or shrub layer), and less by moisture.

Group II includes inhabitants of very wet biotope types with multi-level vegetation cover. They can be classified as hygrobiont woodland species. Biotopes with very wet soils (sometimes inundated) under a multi-level vegetation cover were preferred by 5 species, among which *Craspedosoma rawlinsii* and *Polydesmus denticulatus* (Figs 8 and 9) have a very broad biotope spectrum in total (10 biotope types; eurytopic). *Polyzonium germanicum*, *J. scanicus* and especially *Xestoiulus laeticollis* occur in fewer types (Figs 10 to 12). With the exception of *J. scanicus*, which lives in five very different biotope types, they can be characterised as stenotopic. However, all five species have in common a preference for floodplains and swamp forests (in Figs 10 to 12; the fourth biotope type).

Group III consists of five species which inhabit wet to humid biotope types with multi-level vegetation cover. They can be characterised as hygrobiont woodland species. With the exception of *Nemasoma varicorne* (stenotopic, Fig. 14) all these species may inhabit seven to nine different biotope types (eurytopic; Figs 13, 15–17).

To group IV belongs the one xerobiont woodland species, *L. belgicus*. It inhabits seven different biotope types (Fig. 18), which results in its characterisation as eurytopic.

Group V are open land species, among which *M. projectum kochi* is the only species of those investigated. It occurs in five biotope types (Fig. 19) which are very different in vegetation cover and moisture level, and is therefore assessed as eurytopic.

Group VI consists of xerobiont open land species. Eight species show a clear preference for a combination of very dry/ dry biotope types with single-level vegetation cover (Table 2). Within this species group we can also differentiate between species with a wide biotope spectrum (eurytopic), namely *P. inconstans* (Fig. 21), *Cylindroiulus caeruleocinctus* (Fig. 23) and *Ommatoiulus sabulosus* (Fig. 26), and others with high specialisation for only a few biotope types (stenotopic), namely *O. pilosus* (Fig. 27), *Megaphyllum unilineatum* (Fig. 25), *Choneiulus palmatus* (Fig. 22), *Melogona voigtii* (Fig. 20), and *Kryphioiulus occultus* (Fig. 24).

B. superus occurs in very wet biotope types with variable vegetation cover (group VII), and therefore cannot be classified as a woodland or open land species. The species is eurytopic, but with a preference for very wet and humid places (Table 2, Fig. 28).

M. germanica in group VIII shows no tendency to prefer any biotope type (Table 2, Fig. 29).

Table 3. Ecological characterisation of selected Central European diplopods in Saxony-Anhalt.

Species	General Preference	Main Preference	Special Preference
<i>Glomeris undulata</i> var. <i>conspersa</i>	eurytopic	woodland species	with preference for xeric shrub societies
<i>Glomeris hexasticha</i>	eurytopic	woodland species	with preference for xeric shrub societies
<i>Glomeris marginata</i>	eurytopic	woodland species	without clear preferences
<i>Julus scandinavius</i>	eurytopic	woodland species	without clear preferences
<i>Leptoiulus proximus</i>	eurytopic	woodland species	without clear preferences
<i>Proteroiulus fuscus</i>	eurytopic	woodland species	without clear preferences
<i>Allajulus nitidus</i>	eurytopic	hygrobiont woodland species	without clear preferences
<i>Craspedosoma rawlinsii</i>	eurytopic	hygrobiont woodland species	with preference for floodplains, riparian woody sites and deciduous woods
<i>Polydesmus angustus</i>	eurytopic	hygrobiont woodland species	without clear preferences
<i>Polydesmus denticulatus</i>	eurytopic	hygrobiont woodland species	without clear preferences
<i>Polyzonium germanicum</i>	stenotopic	hygrobiont woodland species	with preference for floodplains and swamp forests
<i>Julus scanicus</i>	eurytopic	hygrobiont woodland species	with preference for floodplains and swamp forests
<i>Tachypodoiulus niger</i>	eurytopic	hygrobiont woodland species	without clear preferences
<i>Unciger foetidus</i>	eurytopic	hygrobiont woodland species	without clear preferences
<i>Xestoiulus laeticollis</i>	stenotopic	hygrobiont woodland species	with preference for floodplains and swamp forests
<i>Nemosoma varicorne</i>	stenotopic	hygrobiont woodland species	without clear preferences
<i>Brachydesmus superus</i>	eurytopic	hygrobiont	with preference for floodplains and swamp forests, often synanthropic
<i>Leptoiulus belgicus</i>	eurytopic	xerobiont woodland species	with preference for thermophilous oak woods and xeric shrub societies
<i>Megaphyllum projectum kochi</i>	eurytopic	open land species	without clear preferences
<i>Cylindroiulus caeruleocinctus</i>	eurytopic	xerobiont open land species	with preference for fields and fallows
<i>Ommatoiulus sabulosus</i>	eurytopic	xerobiont open land species	without clear preferences
<i>Polydesmus inconstans</i>	eurytopic	xerobiont open land species	without clear preferences
<i>Mycogona germanica</i>	eurytopic	–	without clear preferences
<i>Choneiulus palmatus</i>	stenotopic	xerobiont open land species	with preference for xeric/mesoxeric meadows, fields and fallows
<i>Kryphioidiulus occultus</i>	stenotopic	xerobiont open land species	with preference for xeric/mesoxeric meadows, fields and fallows

Species	General Preference	Main Preference	Special Preference
<i>Megaphyllum unilineatum</i>	stenotopic	xerobiont open land species	with preference for xeric/mesoxeric meadows, fields and fallows
<i>Melogona voigtii</i>	stenotopic	xerobiont open land species	with preference for xeric shrub societies
<i>Ophiulus pilosus</i>	stenotopic	xerobiont open land species	with preference for fields and fallows, often synanthropic

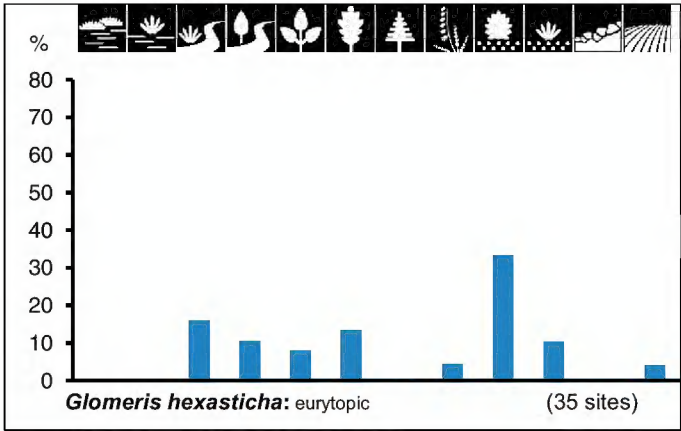


Fig. 2

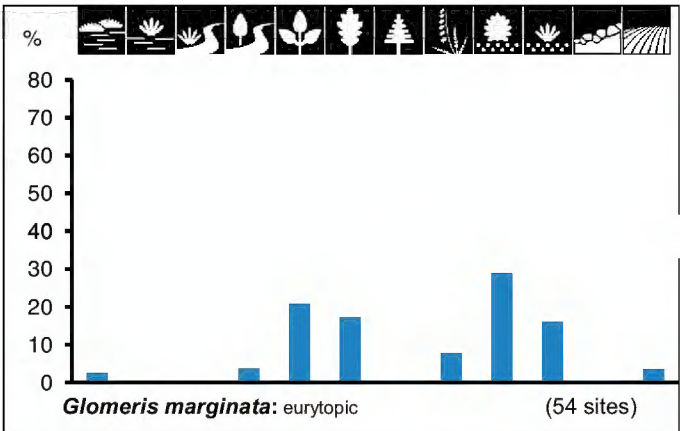


Fig. 3

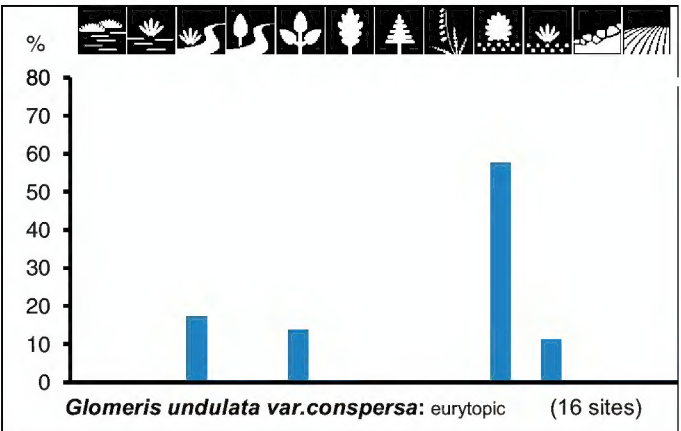


Fig. 4

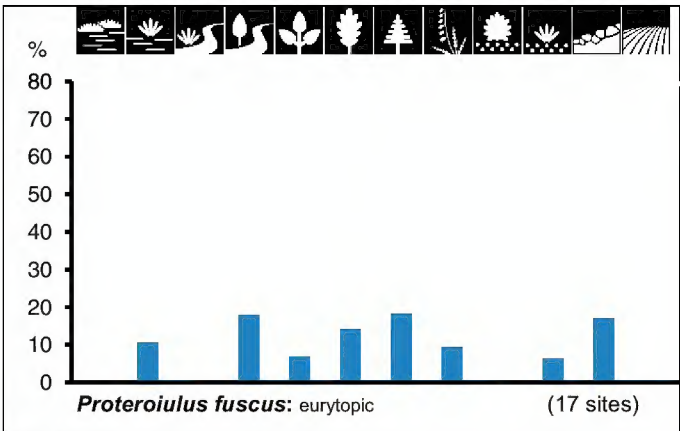


Fig. 5

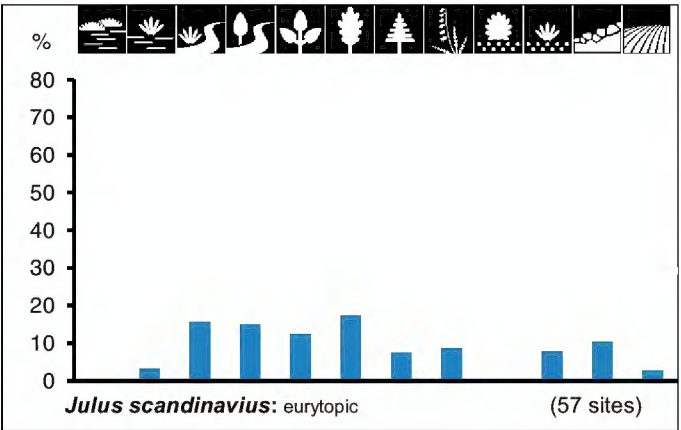


Fig. 6

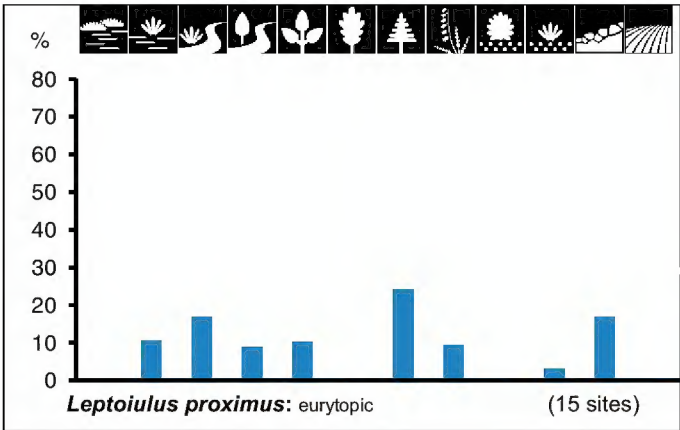


Fig. 7

Figures 2–7. Occurrence of the species of group I (inhabitants of biotope types with multi-level vegetation cover and different moisture) in the 12 biotope types investigated. Numbers of positive samples are given in brackets.

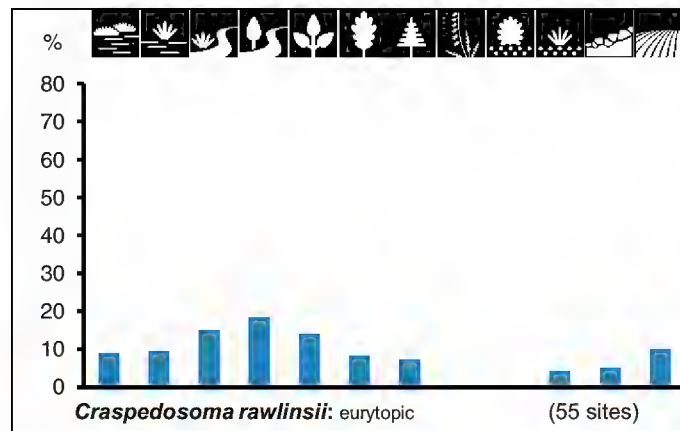


Fig. 8

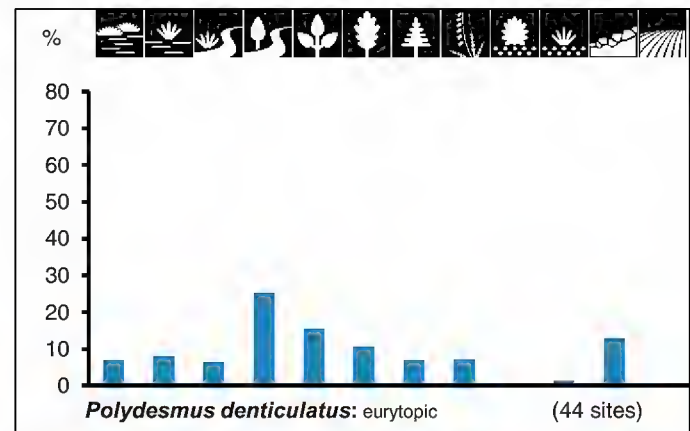


Fig. 9

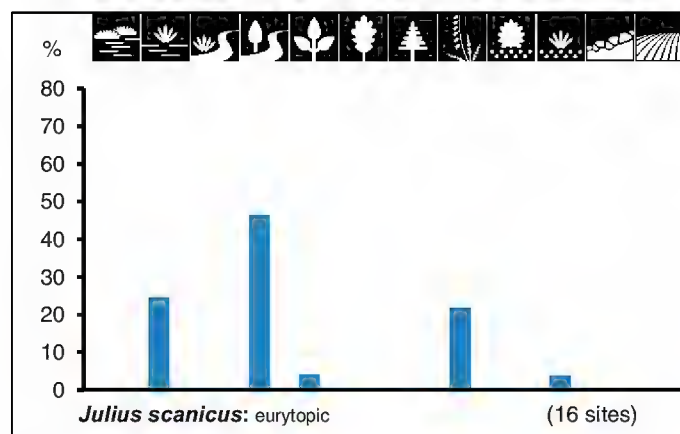


Fig. 10

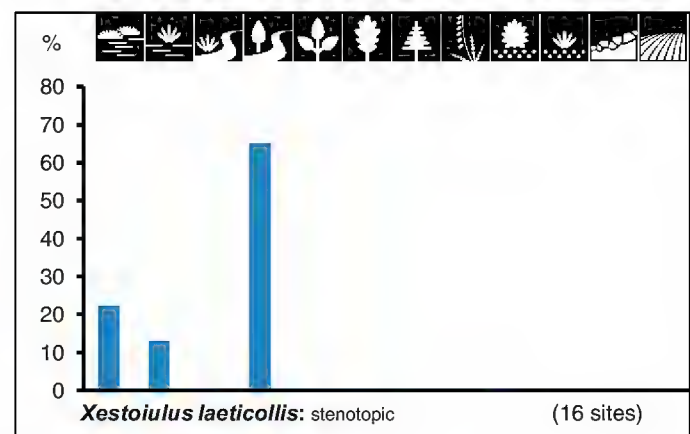


Fig. 11

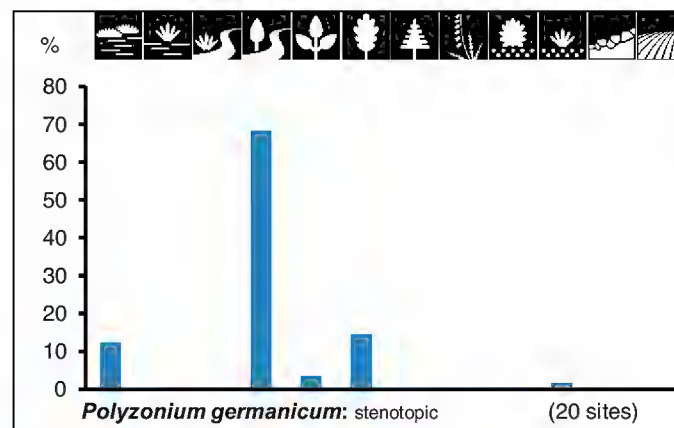


Fig. 12

Figures 8–12. Occurrence of the species of group II (inhabitants of very wet biotope types with multi-level vegetation cover) in the 12 biotope types investigated. Numbers of positive samples are given in brackets.

Distribution of the diplopod families among inhabitant groups

With the exception of Glomeridae, millipede families did not show a preference for a particular group (Table 2). In Polydesmidae and Blaniulidae each species investigated belongs to a different group. In Julidae five species occur in very dry and dry biotope types (group VI, e.g. xeric/mesoxeric/ meadows) with single-level vegetation cover, whereas very wet biotope types with multi-level vegetation cover (group II, e.g. flood-plains) are inhabited by two species. Only one to three julid species belong to the four other groups (I, III, IV and V; Table 2).

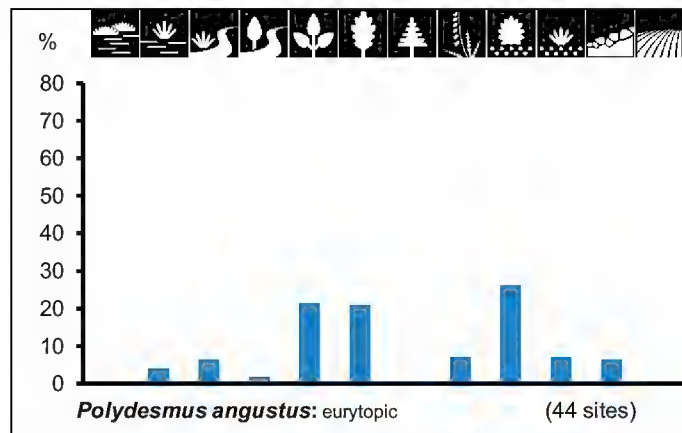


Fig. 13

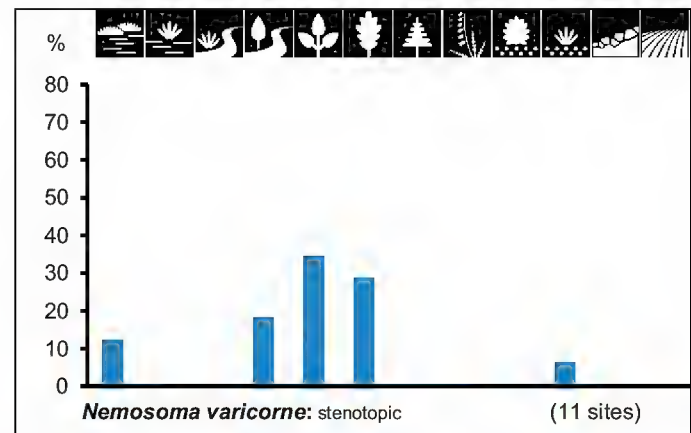


Fig. 14

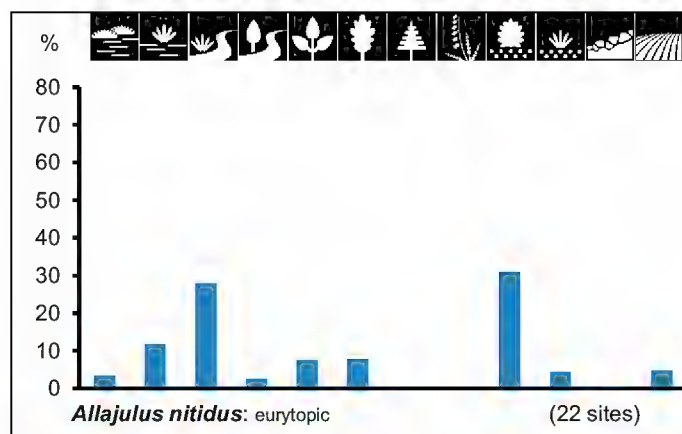


Fig. 15

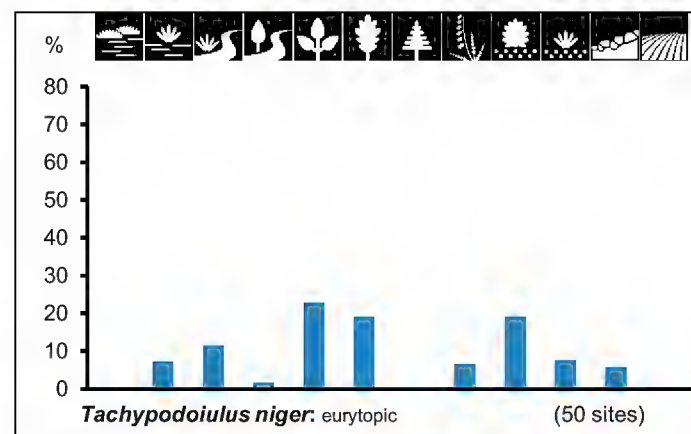


Fig. 16

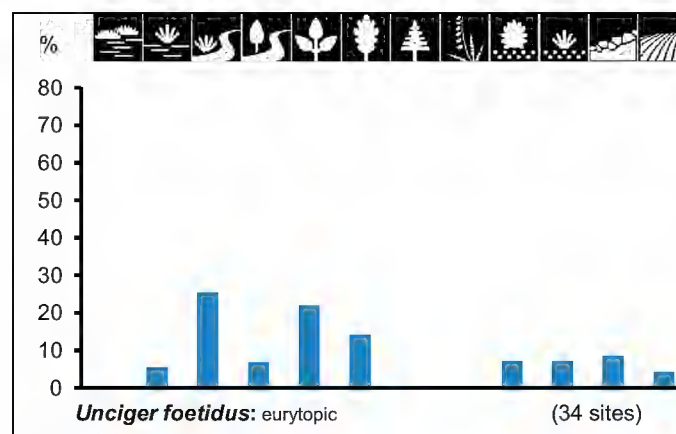


Fig. 17

Figures 13–17. Occurrence of the species of group III (inhabitants of wet to humid biotope types with multi-level vegetation cover) in the 12 biotope types investigated. Numbers of positive samples are given in brackets.

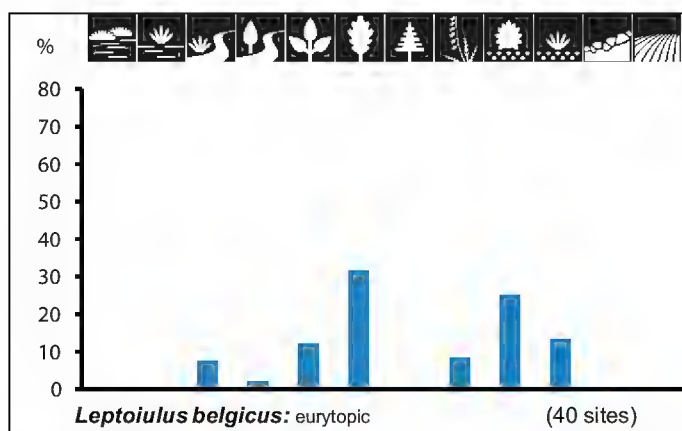


Fig. 18

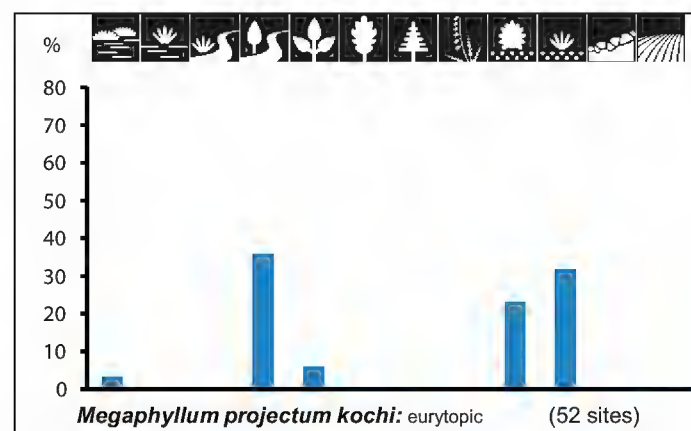


Fig. 19

Figures 18–19. Occurrence of the species of group IV and V in the 12 biotope types investigated. Numbers of positive samples are given in brackets.

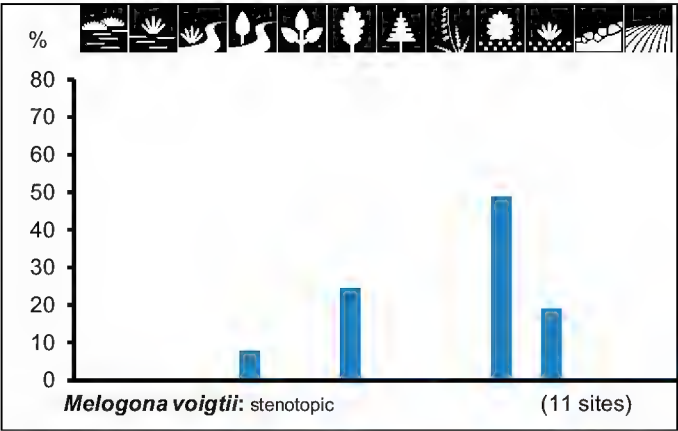


Fig. 20

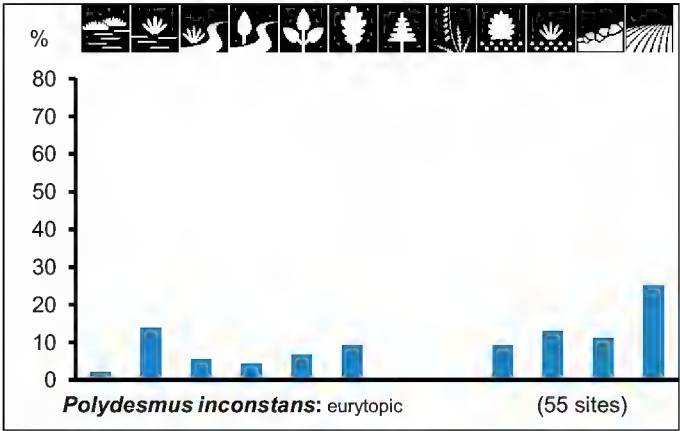


Fig. 21

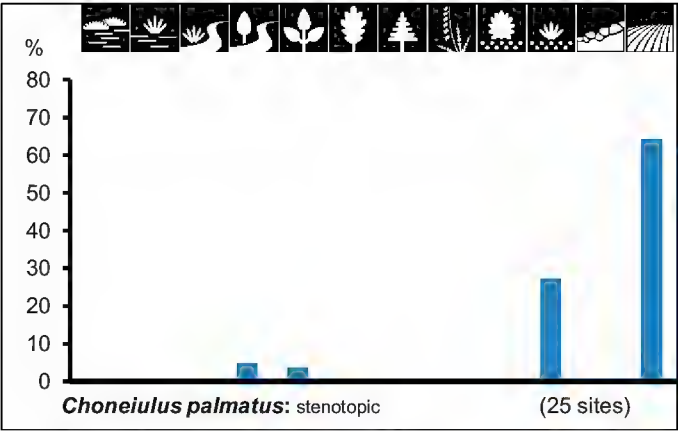


Fig. 22

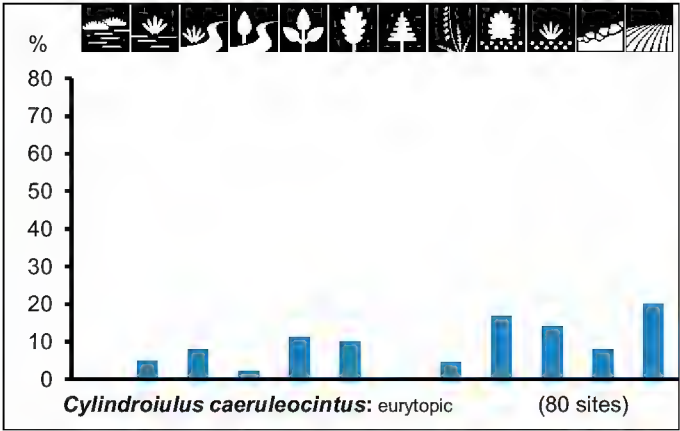


Fig. 23

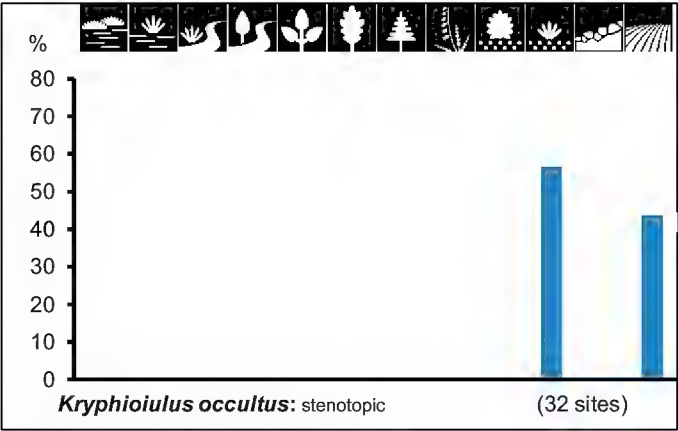


Fig. 24

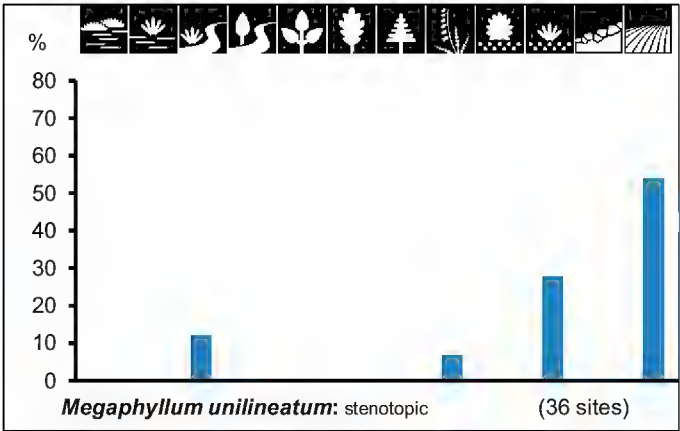


Fig. 25

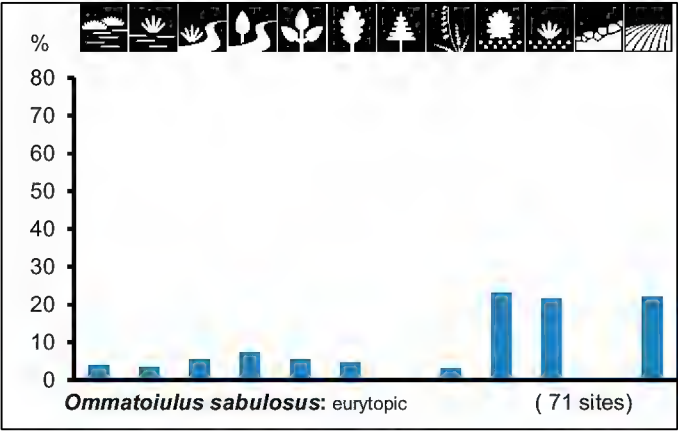


Fig. 26

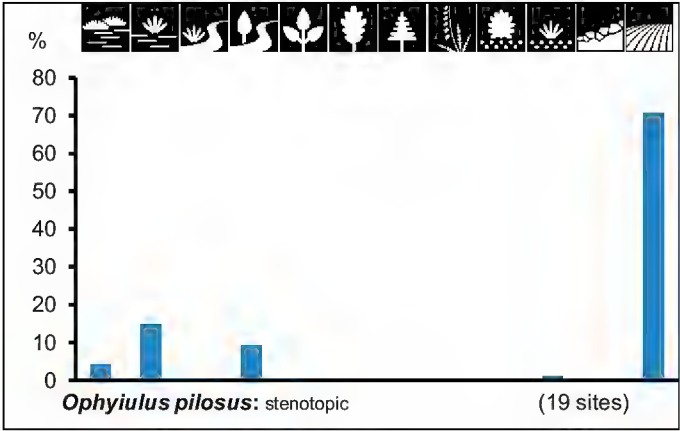


Fig. 27

Figures 20–27. Occurrence of the species of group VI (inhabitants of very dry and dry biotope types with single-level vegetation cover) in 12 biotope types investigated. Number of positive samples are given in brackets.

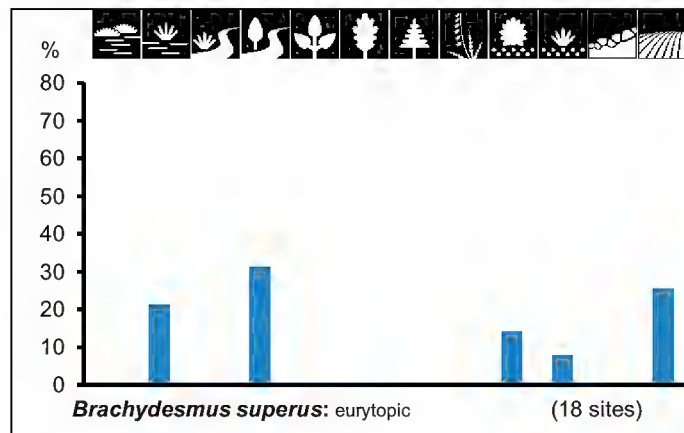


Fig. 28

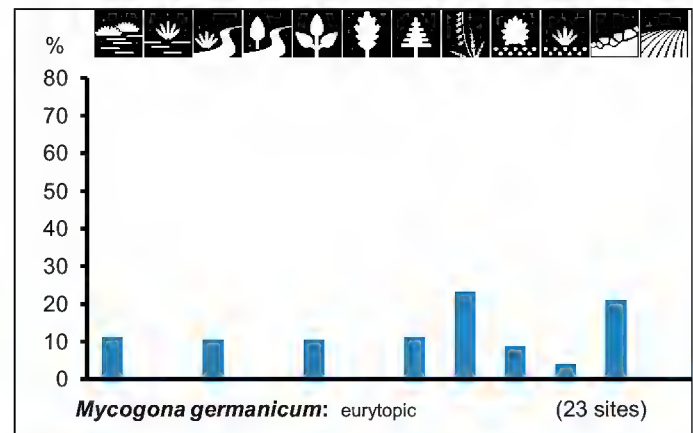


Fig. 29

Figures 28–29. Occurrence of the species of group VII and VIII in the 12 biotope types investigated. Number of positive samples are given in brackets.

Discussion

All species of group I (different moisture levels/multi-level vegetation) prefer biotope types without direct insolation due to a multi-level tree and/or shrub layer. Literature data characterise these species as eurytopic woodland species or ubiquists (e.g. Dunger and Steinmetzger 1981, Kime 2004, Lee 2006, Kime and Enghoff 2011). It is remarkable that if the species occur on xeric or mesoxeric meadows, in most cases the successional shrub stages are more frequent inhabited by the species *Glomeris marginata* and *Glomeris undulata* var. *conspersa*. *Autecological assessment: eurytopic woodland species.*

The Main Preferences of the species belonging to group II (very wet/multi-level vegetation) agree with data from the literature (Schubart 1934, Voightländer 1995, Spelda 1999, Hauser and Voightländer 2009, Kime and Enghoff 2011). Therefore *C. rawlinsii* and *J. scanicus* are discussed as representatives.

Craspedosoma rawlinsii Leach, 1815 (Central European). *C. rawlinsii* is one of the few species for which autecological studies exist. Haacker (1968a) described the species as hygrophilic with low tolerance to dryness and high temperatures. This is confirmed by the species' Main Preference as assessed in the present study. However, different opinions exist in the literature about the habitat requirements of *C. rawlinsii*. On the one hand, riparian, shady, wet or humid woodlands are often recorded (e.g. Harding and Jones 1994; Haacker 1968a, 1968b; Korsós 1997; Wytwer 1997; Zerm 1997; Berg et al. 2008). On the other hand, the species is likewise frequent in mesoxeric and xeric meadows and even heavy metal- contaminated meadows, as well as abandoned fields (Brocksieper 1973, Fründ and Ruszowski 1989, Handke and Handke 1989, Voightländer 2003b, Voightländer and Düker 2001). On land reclaimed from brown coal mining the species is one of the first colonisers (Neumann 1971; Dunger and Voightländer 1990, 2009). Verhoeff (1912) described a “macroductylic variation”, *C. simile oblongosinuatum*, which was said to prefer dry, warm habitats. Comprehensive investigations show that such a form does not exist in reality (Hauser 2004). *C. rawlinsii* is in fact characterised by an enormously broad ecological potency. Its occurrence

in extreme habitats also suggests a high competitive ability for this annual/biannual species. *Autecological assessment: eurytopic woodland species with a preference for swamp forests, riparian woody sites and deciduous woodlands.*

Julus scanicus Lohmander, 1925 (Central European with two distinct south/north western distribution areas and an isolated area in Latvia and Belarus). Especially in its southern distribution area, this species occurs mostly in floodplains and humid deciduous woodlands (Gruber 2007) whereas in its northern distribution area, dry woodlands (Sweden, Schubart 1934), dry shrub heath and mesoxeric sites are added (Fig. 10). On the German Baltic Sea coast and in Scandinavia, anthropogenically influenced sites are also (but seldom) populated (Andersson et al. 2005; SMNG collection). Golovatch (1992) considered the species in the territory of the Russian Plain as “purely synanthropic”, whereas Chotko and Striganova (1975) found the species especially common in bog-reclaimed soils. *Autecological assessment: eurytopic, hygrobiont woodland species with preference for floodplains and swamp forests.*

Within group III (wet to humid/multi-level vegetation) we found species which were characterised as eurytopic or woodland species, most abundant in woodland litter and decaying wood (Haacker 1968a, 1970; Dunger and Steinmetzger 1981; Spelda 1999; Jeekel 2001; Kime 2004; Kime and Enghoff 2011), in agreement with the present study.

Tachypodoiulus niger (Leach, 1815) (North West European). Experimental results are that *T. niger* is a dry-resistant, xerophilous and cool temperature-preferring species (Haacker 1968a) with a little freezing-tolerance (David and Vannier 1997). Under natural conditions the species is mostly found at woody sites which indicates an assessment as a stenoecious (Thiele 1959, Haacker 1968a) or eurytopic (Thiele 1968, Brocksieper 1976, Lee 2006) woodland species. Literature data (Becker 1975, Dunger and Steinmetzger 1981, Spelda 1999) support the latter opinion, as well as the results presented in Fig. 16. In the Netherlands the species is eurytopic in very different habitats (Berg et al. 2008). Over its whole distribution area *T. niger* seems to avoid synanthropy. *Autecological assessment: eurytopic, hygrobiont woodland species.*

Especially remarkable and worthy of discussion are *L. belgicus* and *M. projectum kochi*. Both species demonstrated a special autecological behaviour in the present investigation. They are the only representatives of groups IV and V respectively.

Leptoiulus belgicus (Latzel, 1884) (West European with eastern limit of its distribution area in Central Germany). In Saxony-Anhalt this species is most frequent in dry thermophilous oak forests, in shrub associations and in mesoxeric/xeric meadows. The species shows a conspicuously high fidelity to shrub associations, not only in the present investigation area but also in Thuringia (Dunger and Steinmetzger 1981) and in West German brown coal mining areas (Neumann 1971, Bode 1973). There *L. belgicus* occurs only in the shrub or pre-woody stages of afforested sites, but not on freshly heaped sites without vegetation or in the neighbouring woodlands. In the Netherlands *L. belgicus* also lives only in relatively open land, young plantings and afforestation sites (Berg et al. 2008). It seems not only to tolerate dry conditions, but even to prefer these. Records from Southwest Germany suggest a higher heat requirement (Spelda 1999).

Autecological assessment: eurytopic, (thermophilous) woodland species with particular preferences for thermophilous woodlands, shrub associations and mesoxeric/xeric meadows.

Megaphyllum projectum kochi (Verhoeff, 1907) (South-East European with north-western limits of its distribution area in Germany). According to Haacker (1968a) this species is xerophilous with a temperature preference between 22 and 26°C. In most cases *M. projectum* inhabits bogs, moorland, floodplains and swamp forest as well as diverse woodland types (Loksa 1979, Wytwer 1997, Decker and Hannig 2009, Berg et al. 2008). Therefore it has previously been classified as a stenotopic woodland species. However, this means that the species has dispersed following its temperature preference and against its moisture preference (Haacker 1968a). In the investigations in Saxony-Anhalt xeric/mesoxeric meadows and their successional shrub stages as well as floodplains, bogs and deciduous woodlands are inhabited by *M. projectum*. In South Bohemia the species occurred especially in a meadow and an abandoned field in high abundances (Tajovský 1990). The assessment as a stenotopic woodland species (Haacker 1968a) must be revised. The ecological potential of this species seems to be broader than previously realised. *Autecological assessment: eurytopic open land species.*

Group VI (very dry to dry/single-level vegetation) contains open land species which are stenotopic (*K. occultus*, *M. unilinum*, *C. palmatus* and *O. pilosus*) as well as eurytopic (*C. caeruleocinctus*, *P. inconstans* and *O. sabulosus*). With the exception of *C. caeruleocinctus* and *O. sabulosus* all these species will be discussed.

Kryphioidius occultus (C. L. Koch, 1847) (Eastern European). Over its whole distribution area *K. occultus* shows a change in habitat preference from south to north. In southern parts (Romania, Hungary) it lives in shrub associations and thermophilous woodlands (*Quercetum pubescentis*) (Loksa 1966). In the Czech and Slovak Republics, Austria and in the southern part of Germany and Poland the species is often found in warm open habitats on calcareous ground (xeric and mesoxeric meadows). More to the north *K. occultus* often prefers anthropogenically influenced sites such as gardens, parks and cemeteries. In Sweden, in its most northern distribution area, the species is exclusively found in towns (Andersson et al. 2005). *Autecological assessment: stenotopic, xerobiont open land species with preference for xeric/mesoxeric meadows and fields/fallow.*

Megaphyllum unilineatum (C. L. Koch, 1838) (East European). This extreme xerothermic species is typical for open sites in its whole distribution area, and also inhabits the south-eastern open woodlands with their dry and warm microclimate (Loksa 1966). In Eastern Germany including Saxony-Anhalt the species shows a high tendency to inhabit fields and fallows (Fig. 25; Hauser and Voigtländer 2009). It is highly unlikely that individuals migrate from adjacent grasslands into the fields, because their dispersal usually does not exceed a few meters (Haacker 1968a). In laboratory experiments the species is dry-resistant and moisture-indifferent with a temperature preference between 22 and 30°C (Haacker 1968a). *Autecological assessment: stenotopic, xerobiont open land species with preference for xeric/mesoxeric meadows, fields and fallows.*

Ophiulus pilosus (Newport, 1842) (Northwestern and Central European). Within its northern distribution area (its distribution is disjunct – see Kime 1990) *O. pilosus*

has a remarkable ecological behaviour. In Western Germany and Great Britain the species can be found in floodplains, brook forests and humid deciduous forests (Schubart 1928), but there it also occurs on pioneer and ruderal sites, dumps and in meadows, gardens, parks, field hedges and other synanthropic habitats (Fründ and Ruzkowski 1989; Decker and Hannig, pers. comm. 2011). In those areas *O. pilosus* is therefore eurytopic. In Central Germany (Saxony-Anhalt) occurrences in fields dominate (Fig. 27). Further to the east or northeast, the habitat preference changes again, with *O. pilosus* almost exclusively at synanthropic localities. *Autecological assessment: stenotopic, xerobiont open land species with preference for fields and fallows (Eastern Germany only).*

Choneiulus palmatus (Němec, 1895) (European). In Central Europe the species is nearly exclusively synanthropic. German records from near-natural sites are the exception and come exclusively from warm regions (e.g. Rhine-Main-area – Haacker 1968b) or warm open habitats (e.g. mesoxeric meadows in Thuringia – Seifert 1968, Peter 1984; SMNG collection). The latter finding agrees with occurrences in Saxony-Anhalt (Fig. 22). Records from swamp forests as recorded in the present study are very rare (Berg et al. 2008). *Autecological assessment: stenotopic, xerobiont open land species with preference for xeric/mesoxeric meadows, fields and fallows.*

Polydesmus inconstans Latzel, 1884 (Central European). This species shows variable ecological behaviour over its distribution area. At the western boundary (Western Germany, the Netherlands) *P. inconstans* is very rare and occurs exclusively at synanthropic localities (Thiele 1968, Fründ and Ruzowski 1989, Berg et al. 2008, Decker et al. 2009). In Eastern Germany the species is very common and can also be found in “natural” woodlands (Schubart 1957, Steinmetzger 1982, Voigtländer and Dunger 1992). More to the east it becomes synanthropic again (Kime and Enghoff 2011). Thus this species is very eurytopic with a tendency to more open and dry biotope types as shown in the present investigations. The high ecological potential enables the species to colonise very freshly reclaimed land after brown coal mining nearly without vegetation (e.g. Neumann 1971; Dunger and Voigtländer 1990, 2009). Over the whole of its distribution area *P. inconstans* shows high tolerance to disturbance. *Autecological assessment: eurytopic, xerobiont open land species.*

Brachydesmus superus Latzel, 1884 (European). Originally in forests, especially in deciduous woodland (Kime and Enghoff 2011); frequent in humus-rich humid soils (Jeekel 2001). *B. superus* has spread far beyond its original distribution area and has become quite common in cultivated land. The species is often found at synanthropic locations, especially towards the northern and eastern periphery of its distribution area. *B. superus*, the only species of group VII, occurs in Saxony-Anhalt in different biotope types, mostly in floodplains and fresh meadows, but is also found in fields and fallows in large numbers. Such preferences are also mentioned by Spelda (1999) for Baden-Württemberg, Germany. In contrast, especially in Thuringia the species was often found in xeric and mesoxeric meadows (Hauser and Voigtländer 2009), but over the whole distribution area a preference of this species for moist biotope types is indisputable (e.g. Berg et al. 2008). *Autecological assessment: eurytopic, hygrobiont species with preference for floodplains and swamp forests, often synanthropic.*

Mycogona germanica (Verhoeff, 1892) (Central European). This species occurs primarily in the Central European Uplands (Germany, Czech Republic, Poland, Switzerland, Belgium, the Netherlands) with a clear preference for woodland (spruce forests). In Saxony-Anhalt it is limited to the Harz mountain range and its foreland. There the species inhabits bogs, gravel areas, dwarf-shrubs heaths, mesoxeric meadows and other more open habitats in addition to woodlands (Voigtländer 1999, 2003b). In contrast to the main distribution area *M. germanica* is very eurytopic in Saxony-Anhalt. In the present investigation, it is the only species showing neither an influence of the biotope type's moisture nor the density of vegetation cover (group VIII). *Autecological assessment: eurytopic (woodland) species.*

Conclusion

Studies on ecological preferences of soil animals can yield different results for one and the same species if they are based on too small a number of replicates. This is due to the fact that many species have the potential to tolerate unfavourable conditions. They can live in “bad” habitats but they do not prefer them (e. g. *Craspedosoma*). Only investigations based on a large number of observations as in the present study (27,000 individuals from 175 sites), concentrated on a relatively small investigation area, may yield an approximation to reality. To focus such investigations on a smaller area, at first, seems necessary because the influence of the climatic region on the ecological behaviour of the species should be taken into consideration. Convincing examples for such changes in preferences of chilopod species when considering a larger area of distribution are *Cryptops anomalans*, *Geophilus electricus* and *Strigamia acuminata* (Ghilarov and Folkmanová 1957, Ghilarov 1964, Voigtländer 2005). The present study shows similar changes across larger areas for *J. scanicus*, *K. occultus*, *M. unilineatum*, *O. pilosus* and *P. inconstans*.

In small-scale area studies, e.g. in a comparison of different regions within Germany (Hauser and Voigtländer 2009), differences in the frequency of distinct preferences can likewise be detected. However, as the trends remain the same as in the large-scale studies, such minor differences do not affect the overall pattern of ecological preferences, as revealed in the present investigation.

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